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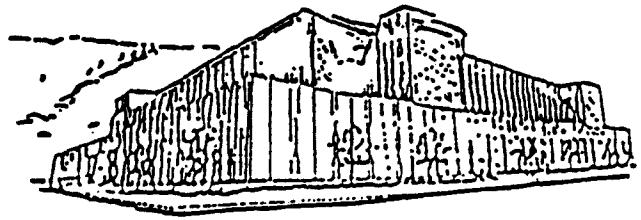
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Transplanted whitebark pine regeneration: the response of different
populations to variation in climate in field experiments

by

Janet Howard


B.A., California State University, Stanislaus, 1984

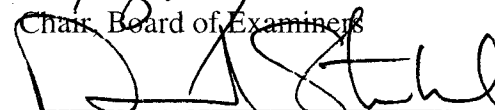
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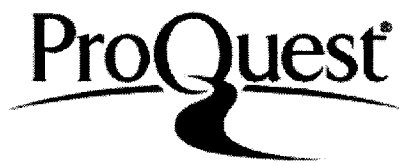


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Transplanted whitebark pine regeneration: the response of different populations to variation in climate in field experiments

Advisor: Ragan M. Callaway

Whitebark pine (*Pinus albicaulis* Engelm.) is an important species in subalpine and timberline forests of western North America. Due to synergistic effects of several agents including an exotic blister rust, whitebark pine is in decline throughout nearly its entire range. Decline of whitebark pine has generated interest in transplanting programs; however, little is known of the ability of whitebark pine seedlings to adapt when transplanted on sites that differ from that of their origin. This study compares survivorship, growth, biomass accumulation, and carbon isotope discrimination among four whitebark pine populations planted on three sites that vary in climate. Two of the populations were from seed sources with apparent blister rust resistance. After 2 years in the field, survivorship, growth, biomass allocation, and carbon isotope discrimination differed among sites. Height ($P=0.003$), stem diameter ($P<0.001$), and leaf area ratio ($P=0.01$) differed among populations. There were no significant differences between populations in carbon isotope discrimination. Site \times population interaction effects were significant for height and stem diameter ($P<0.001$), all biomass allocation variables, and for carbon isotope discrimination ($P=0.04$). Performance of transplanted populations was not correlated with site of origin. These results suggest that whitebark pine populations can successfully be transplanted outside their area of origin, but populations appear to have site-specific morphological and physiological adaptations. Relocating blister rust resistant seedlings to new areas may interfere with naturally evolving populations, and is not recommended in areas where whitebark pine populations are not depressed. However, in areas where populations are in severe decline, artificial regeneration with blister rust resistant seedlings may be the only option in retaining whitebark pine as an important member of the plant community.

TMC

Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) is a dominant species in many subalpine and timberline forests of western North America, with important effects on biodiversity in subalpine ecosystems (Primack 1998). The seeds are an important, highly nutritious food source for several species of birds and mammals including the threatened grizzly bear (*Ursus arctos horribilis*) (Lanner & Gilbert 1994, Mattson et al. 1992.) Whitebark pine communities are important grizzly bear habitat. Increasing the number of mature, cone-producing whitebark pine available for grizzly bear has been identified as crucial for grizzly bear recovery (Kendall 1994, Mattson & Reinhart 1997). Whitebark pine has important effects on ecosystem function by protecting watersheds by stabilizing rock and soil on steep slopes, by catching and retaining snowpack, and as a shade-intolerant pioneer species after fire (Arno & Hoff 1989).

Whitebark pine has declined rapidly over most of its range due to successional replacement due to fire exclusion, mountain pine beetle (*Dendroctonus ponderosae*) attacks, and an exotic blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh) that infects five-needled white pines (Arno 1976, Hoff & Hagle 1990, Hoff et al. 1994, Keane & Arno 1993, Kendall 1994). Whitebark pine mortality has been extremely high in the Cascade and northern Rocky Mountain ranges (Arno 1976, Hoff & Hagle 1990, Keane & Arno 1993). Populations in Glacier National Park, Montana, have declined by 90% due to synergistic effects of these agents (Kendall 1994). Whitebark pine regeneration has been extremely low because mortality of mature, cone-bearing trees has greatly reduced seed sources (Tomback et al. 1995). Populations in many areas have reached critical lows where mortality of cone-bearing trees greatly exceeds natural regeneration.

Because of the widespread and devastating effects of blister rust on whitebark pine, planting blister rust resistant seedlings may be the only option if whitebark pine is to be retained as an important component of the plant community. There is substantial interest

in developing planting programs using blister rust resistant seedlings to restore whitebark pine populations.

Selecting an appropriate seed source is probably the most important management decision required in order to produce a healthy, fit stand (Meagher & Hunt 1999). Successful large-scale outplanting of whitebark pine may be enhanced by knowledge of genetic variation within and among whitebark pine populations. Whitebark pine is distributed over a large geographic area that encompasses an extremely wide range of soil types and climatic conditions (Arno & Hoff 1990). The potential for site-specific adaptations in whitebark pine is great; however, little is known of genetic variability in whitebark pine (Hoff et al. 1994). Due to its decline, whitebark pine is probably losing genetic variability rapidly. In areas of high rust infection, whitebark pine is undergoing an extreme genetic bottleneck. Blister rust resistance is a rare trait in whitebark pine (Hoff et al. 1994). Average resistance in whitebark pine populations is estimated at 3 to 5% (Hoff et al. 1976, Stephan 1985). Population bottlenecks severely reduce the number of rare alleles in populations, and genetic diversity is important for the long-term ability of populations to survive and respond to genetic selection (Allendorf 1986).

Predicting genetic diversity and population structure of whitebark pine is difficult because several factors that affect gene flow in whitebark pine appear to act both synergistically and antagonistically (Bruederle et al. 1998). Allozyme studies indicate that whitebark pine has low genetic diversity in comparison to other North American pines, and that most genetic diversity is among rather than within populations (Bruederle et al. 1998, Jorgensen & Hamrick 1997). Wind dispersal of pollen and seed dispersal by Clark's nutcrackers (*Nucifraga columbiana* Wilson) appear to facilitate gene flow between whitebark pine populations; however, present decline and fragmented spatial distribution may restrict gene flow in whitebark pine. In fragmented populations, founder effects and genetic drift may result in genetic differences between populations (Tomback & Linhart 1990, Bruederle et al. 1998).

Studies of genetic diversity of traits of adaptive significance have not been conducted on whitebark pine. Traits that regulate the water relations of pines may be highly selected on because water stress often limits conifer seedling establishment and growth in subalpine environments (Cui & Smith 1991, Roe et al. 1970, Peterson & Peterson 1994, Weaver 1994). Annual precipitation is high in subalpine environments of the northern Rocky Mountains, but summer drought is common (Pfister et al. 1977, Weaver & Dale 1974). Water deficits during the growing season are especially stressful for transplanted seedlings because seedlings raised in greenhouses are subject to acute shock when introduced to a natural site (Sun et al. 1996). Because of the long-lasting snowpack, transplanting usually occurs in subalpine environments in early summer and is often followed by severe and prolonged drought. Traits that enhance drought tolerance include leaf-level characteristics that reduce stomatal water loss during photosynthesis (Farquar et al. 1982, Masle and Farquar 1988) and allocational traits such as increasing biomass allocation to roots and stems while decreasing allocation to leaves (Callaway & DeLucia 1994, Callaway et al. 1994). Genetic variation in both biomass allocation and leaf-level physiology has been identified for many conifer species (Callaway et al. 1994, Cregg 1993, Monson & Grant 1989, Zhang & Marshall 1995).

Differences in water-use efficiency have been demonstrated between genera of the pine (*Pinaceae*) family (Barton & Teeri 1993, Zhang & Marshall 1995) and between populations of pine species. Monson & Grant (1989) demonstrated definite, heritable differences in water-use efficiency between ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) populations from an east-west, dry-wet gradient. Whitebark pine appears to be highly drought tolerant (Arno & Hoff 1990, Pfister et al. 1977), but the water relations of whitebark pine are poorly understood. Understanding natural variation in water-use efficiency among populations of whitebark pine may be of particular importance because transplanting programs using rust resistant seedlings may capture only a small portion of the whitebark pine genotype.

How far blister rust resistant whitebark pines can be transplanted from their area of origin is unknown (Hoff et al. 1994). Few planting trials have been attempted with whitebark pine, and these involved seedlings that were not selected for blister rust resistance and were planted within their own provenance (McCaughey 1994). Among-population differences in traits related to drought tolerance in whitebark pine could affect survivorship when rust resistant seedlings are transferred from area of origin. The purpose of this study was to determine if a suite of drought tolerance traits varies between populations and sites in whitebark pine seedlings. I compared traits of survivorship, growth, biomass allocation, and water-use efficiency among four whitebark pine populations transplanted to three sites that varied in climate.

Species

Whitebark pine is distributed in the Coast Ranges of British Columbia, the Cascade Range, the Sierra Nevada, and in the Rocky Mountains from Alberta to Wyoming (Arno & Hoff 1990). The life history of whitebark pine is distinct from other conifers of North America in that its seeds are almost exclusively bird dispersed. The indehiscent cones and large, wingless seeds of whitebark pine require opening and dispersal by Clark's nutcrackers (Lanner & Gilbert 1994, Tomback & Linhart 1990). Whitebark pine is classified in *Cembrae*, a subsection of the subgenus *Strobus* (Critchfield & Little 1966). It is the only *Cembrae* pine native to North America. Clark's nutcrackers carry whitebark pine seeds distances that range from several meters to more than 3 km from parent trees and bury the seeds in groups of 1-15 or more per cache. Seeds in a single cache were usually collected by an individual bird from one parent tree (Tomback 1978, Tomback & Linhart 1990). Clark's nutcrackers consume most of the seed they cache in winter and spring, but unretrieved seeds often germinate and produce solitary or clustered seedlings. Clustered seedlings usually continue to grow as a group and may eventually

fuse at the base (Linhart & Tomback 1983, Tomback 1982, Vander Wall and Hutchins 1983).

The tendency of Clark's nutcrackers to cache whitebark pine in clusters of seed collected from the same parent results in an unusual population structure where individuals within a cluster are more closely related to each other than to individuals in other clusters. Furnier et al. (1987) found that individuals in whitebark pine clusters are related, on average, as half-sibs. The genetic consequences of clumped growth form in whitebark pine are inbreeding and an excess of homozygotes (Jorgensen & Hamrick 1997). Because many different Clark's nutcrackers cache seeds at a site, the result is a genetically heterogeneous pattern of tree clusters, with neighboring clusters no more closely related than are distant clusters. As a result of Clark's nutcracker seed dispersal, whitebark pine populations may be less genetically differentiated than populations of wind-dispersed pine species (Bruederle et al. 1998, Tomback et al. 1992).

Materials and methods

Three study sites were chosen using the following criteria: (1) sites were located on stand-replacement burns resulting from wildland fire, with mineral soil available for planting; (2) sites were located on a latitudinal gradient similar to that of seedling provenances (Table 1); (3) sites were at mid-elevation (1200-2290 m) with southerly exposures (Table 1); (4) whitebark pine was a component of the vegetation prior to the fire; and (5) accessibility. The moisture gradient of the sites from north to south is mesic-dry-wet. Temperature, precipitation, and relative humidity data for the three sites are summarized in Table 3. The Lunch Creek site, hereafter referred to as the wet site, is on the Boise National Forest in central Idaho. The Lunch Creek Fire occurred in 1989 and burned 3880 ha. The habitat type is subalpine fir/pinegrass (*Abies lasiocarpa* (Hook.) Nutt.)/*Calamagrostis rubescens* Buckl.). Soil is granitic with loam texture (Steele et al.

1981). Blister rust was not detected in the area during the course of this study. Unburned forest adjacent to the Lunch Creek study site is in late succession with subalpine fir and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) replacing lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and whitebark pine. Natural whitebark pine regeneration on the burn is sparse. The Sundance Burn (mesic) site is located on the Kaniksu National Forest in northern Idaho. The Sundance Fire occurred in August 1967 and severely burned more than 22,600 ha (Anderson 1989). The habitat type is western hemlock/pachistima (*Tsuga heterophylla* (Raf.) Sarg./*Pachistima myrsinites* (Pursh) Raf.) (Daubenmire & Daubenmire 1968) with mixed western redcedar (*Thuja plicata* Don ex D. Don), subalpine fir, whitebark pine, lodgepole pine, and western white pine (*P. monticola* Dougl. ex D. Don). Soil is granitic with sandy loam texture (Daubenmire & Daubenmire 1968, Stickney 1985). Whitebark pine mortality from blister rust is severe (> 50% basal kill), and there is an approximate 29% infection rate of newly regenerating whitebark pine (Keane & Arno 1993, Tomback et al. 1995). The Smith Creek (dry) study site is located at the headwaters of Smith Creek on the Bitterroot National Forest in western Montana. The Smith Creek Fire occurred in 1988 and burned 49 ha. The habitat type is subalpine fir/smooth woodrush (*Luzula hitchcockii* Hamet-Ahti) with lodgepole pine and minor amounts of Engelmann spruce and whitebark pine. The soil is granitic with sandy loam texture (Pfister et al. 1977). Until a few decades ago whitebark pine was a major seral component of the plant community. Blister rust mortality has increased from light to moderate (20-50% basal kill) in the 1990s, and approximately 90% of mature whitebark pine are infected (Keane & Arno 1993, 1996).

U.S. Forest Service personnel collected whitebark pine seeds between 1991 and 1993 from four populations on latitudinal and moisture gradients. The populations occur in different climates with wet (central Idaho), mesic (northwestern and northeastern Idaho), and dry (western Montana) moisture regimes (Table 2). Mature seeds were harvested

from at least 10 open-pollinated trees per population. Seeds from two of the populations, Gisborne and Lunch peaks, were collected from phenotypically rust resistant parents. Trees on Gisborne and Lunch peaks have been exposed to severe blister rust for decades. Some cone-bearing trees on the Gisborne and Lunch peak sites, including those used as parent trees in this study, show phenotypic rust resistance. Offspring of phenotypically rust resistant trees are expected to have greater than average levels of rust resistance (Hoff et al. 1994). Rust severity in the Saddle Mountain population was low (< 20% basal kill) at time of seed collection (Keane & Arno 1993), and the Snowbank Mountain population showed no symptoms of infection at the time of seed collection. Progeny of Saddle and Snowbank mountain populations are expected to have average susceptibility to blister rust, estimated by Stephan (1985) at 97%. Seeds were stored in freezers at -13°C prior to the study. Seeds were then stratified for 60 days; their seedcoats clipped to break dormancy; sown three to a cell in styroblock containers with a perlite-vermiculite-potting soil mixture; and germinated in a greenhouse. Seedlings were thinned to one per cell after emergence and grown in the greenhouse for 1 year.

At 1 year of age, 90 seedlings per population were transplanted between 6 and 16 June 1995 at each of the three study sites (for a total of 1080 seedlings) on three linear transects per site. Plastic mesh seedling protector tubes reinforced with stakes were placed around seedlings to deter herbivores.

Survivorship and growth data were collected for all seedlings. Survivorship was measured at the end of the first and second growing seasons following planting, in late September of 1996 and 1997. Height and stem diameter were measured in late September 1997. Stem diameter measurements were taken at the root crown. Number of seedlings per population measured for growth at the wet site were: n=44 for northwestern Idaho, 26 for northeastern Idaho, 32 for western Montana, and 43 for central Idaho. For the mesic site, n=45, 21, 30, and 32, respectively. For the dry site, n=28, 32, 33, and 27, respectively. Twelve seedlings per population were chosen

randomly and harvested from each study site (144 seedlings total) for aboveground biomass allocation and carbon isotope discrimination analyses. For biomass allocation analyses, the harvested plants were divided into stems and needles. One-sided leaf area was determined from 10 current-year needles per seedling prior to oven drying. Stems and needles were dried at 80°C for 24 h, and weighed. These data were used to calculate leaf area ratio (LAR, m² leaf/g aboveground plant) and leaf mass ratio (LMR, g leaf/g aboveground plant) (Evans 1972).

Water-use efficiency (ratio of photosynthesis to water loss) is one measure of drought tolerance. Farquhar et al. (1982) suggested that in plants with C₃ photosynthesis, plants that discriminate against ¹³CO₂ relative to ¹²CO₂ show greater water-use efficiency than plants showing less discrimination. Water-use efficiency is calculated as

$$A/E = (c_a - c_i)/(1.6 \cdot w)$$

where A is net photosynthesis, E is transpiration, c_a is ambient CO₂ concentration, c_i is leaf intercellular CO₂ concentration, 1.6 is the ratio of the diffusion coefficients of H₂O to CO₂ in air, and w is the water vapor gradient between leaf and air. Plants with low c_i concentrations tend to show high rates of water-use efficiency and drought tolerance. Long-term estimates of c_i can be made using carbon isotope analysis.

For carbon isotope discrimination analysis, 10 unshaded, current-year needles per seedling were oven-dried at 80° C for 24 h, ground to a fine powder with a ball mill, and subsampled. Isotopic signature was determined by the University of Georgia, Institute of Ecology, on CO₂ from combusted subsamples using a Finnigan delta C mass spectrometer (precision = 0.04‰). Long-term estimates of intercellular CO₂ concentration (c_i) were calculated as

$$c_i = c_a \cdot ({}^{13}\text{C}_{\text{air}} - {}^{13}\text{C}_{\text{leaf}} - a)/(b-a)$$

where ${}^{13}\text{C}_{\text{air}}$ is the carbon isotope ratio of the air, ${}^{13}\text{C}_{\text{leaf}}$ is the carbon isotope ratio of the leaf, a is the discrimination associated with the slower diffusion rate of ¹³CO₂ (4.4‰), and b is net discrimination against ¹³CO₂ associated with RuBP carboxylase (27)

(Farquhar et al. 1982).

Isotopic composition of the subsample was calculated as

$$^{13}\text{C} (\text{‰}) = R_{\text{sample}} R_{\text{standard}}/R_{\text{standard}}) \times 1000$$

where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$ in the sample and standard, respectively.

Two-way analysis of variance was used to compare site, population, and site \times population interaction effects on all dependent variables (Sigmaplot 1997). Independent variables were fixed in the ANOVA model. Twenty outliers that represented very small seedlings (< 3 cm) were dropped from height data for normalization. Other dependent variables were normally distributed.

Results

Seedling survivorship across sites averaged 40% the first year after transplanting (Fig. 1). Summer precipitation in first field growing season was 49% or less than normal at all sites (Table 3, Fig. 1). Precipitation was still below normal in the second year of study on all sites except the dry, but seedling mortality rate on all study sites slowed greatly in the second year of study (Fig. 1).

Survivorship among populations varied significantly among sites (chi-square, $P=0.05$). Mean survivorship across populations the in second autumn after planting was 33% greater on the wet site compared to the dry site (Fig. 1). Population survivorship ranking across sites from greatest to least was northwestern Idaho (from a mesic site), central Idaho (wet), western Montana (dry), and northeastern Idaho (mesic) (43, 38, 35, and 29%, respectively). Even though survivorship differed among populations and sites, populations did not perform better in climates that were similar to climates of their place of origin. For example, the northeastern Idaho (wet) population had the lowest survivorship of all four populations on the wet and mesic sites, but ranked second in

survivorship on the dry site (Fig. 1).

Site, population, and site \times population interaction effects were strongly significant for height and stem diameter growth (Table 4). Across populations, mean height was 9% greater and stem diameter 13% greater on the wet site compared to the dry site (Fig. 2). Across sites, seedlings from northwestern Idaho (mesic) gained the most height, and seedlings from central Idaho (wet) gained the least. There was a 14% difference in mean height between the two populations. There was no clear geographic pattern to height and stem diameter growth relative to area of seedling origin. Mean stem diameter across sites was greatest for the northwestern Idaho (mesic) and western Montana (dry) populations (4.13 and 4.14 mm, respectively). The mean stem diameter of northwestern Idaho (mesic) and western Montana (dry) populations was 11% greater than that of the northeastern Idaho (mesic) population, which gained the least average stem diameter (3.58 mm) of the four populations.

Site and site \times population interaction effects were significant for total aboveground biomass and for all biomass allocation variables (Table 5). Population effects were insignificant for total aboveground biomass and for all biomass allocation variables except LAR (Table 5). As for survivorship, there was no consistent relationship between population origin and aboveground biomass accumulation at different sites. At the central Idaho (wet) site, for example, the central Idaho (wet) population had the lowest biomass of all populations at that site. In contrast, the northwestern Idaho (mesic) population showed superior biomass compared to other populations at the central Idaho (wet) site (Fig. 3). At the dry site, the northeastern Idaho (mesic) population accumulated less biomass than the other three populations. Seedling biomass was 64% less at the dry site compared to the wet site. Across sites, seedlings at the dry site allocated a greater percentage of biomass to stem tissue over leaf tissue compared to seedlings at the wet site (Fig. 4). Mean LMR was similar on wet and mesic sites (0.59 g leaf/g aboveground plant), and was significantly different from LMR on the dry site (0.54 g leaf/g

aboveground plant) (Table 5, Fig. 4).

There were significant differences in LAR between sites ($P=0.05$) and between populations ($P=0.01$) (Table 5). Seedlings at the wet and mesic sites allocated proportionately more leaf surface area per gram of aboveground mass compared to seedlings at the dry site. LAR was greatest on the mesic site and least on the dry site, with a 23% difference in LAR between the two sites (Fig. 4). Seedlings from northeastern Idaho (mesic) site had 32% greater LAR than seedlings from western Montana (dry).

The site effect was significant for carbon isotope discrimination ($P=0.0008$) and site \times population interaction effects for carbon isotope discrimination ($P=0.04$). Carbon isotope discrimination was least, and water-use efficiency greatest, at the dry site (Fig. 5). Carbon isotope discrimination across sites was 5% greater on the wet site compared to the dry site. There were no significant differences between populations for carbon isotope discrimination.

Discussion

My results indicate that whitebark pine populations have site-specific survivorship, growth, morphological, and physiological characteristics. These results suggest that translocating seedlings may introduce genetic differences into naturally evolving populations. However, the lack of strong, predictable relationships between climate and population response, or consistently better performance of populations near their place of origin, suggests that transplanting over long distances may not have substantial effects on the performance of transplants.

There are dangers in using seedling characteristics such as rapid growth to predict long-term plantation success. Seed transfer should be based on a balance between growth and the ability of the trees to withstand environmental pressures over their life span

(Meagher & Hunt 1999) — potentially more than a millennium for whitebark pine (Perkins & Swetnam 1996). Environmental regimes may change substantially as a stand of long-lived conifers such as whitebark pine ages (Hiebert & Hamrick 1983). Even small fluctuations in climate may affect survivorship and growth of transplants during the establishment period. For example, seedlings that gain rapid height growth and allocate much of their biomass to leaves when the first few years after planting are followed by favorable precipitation may show poor survivorship and growth when site conditions become drier. On dry sites, slow growth and biomass allocation to nonphotosynthetic tissue may be advantageous in the long term due because respiration rates and water losses are reduced.

Drought is the most common cause of mortality on conifer plantations (Sun et al. 1996). Severe summer drought following transplanting was probably responsible for low seedling survivorship in the first year of study. Young seedling age (1 year) and small height ($m=8.1$ cm) at time of transplanting probably also contributed to low survivorship. Even in greenhouse conditions, whitebark pine seedlings attain little height growth in their first year, and an additional year in the greenhouse may have improved first-year survivorship of the transplants. Even so, mortality rates appear to be slow to stabilize in transplanted whitebark pine. McCaughey (1994) reported 91% survivorship of seedlings one year after transplanting greenhouse-grown, two-year-old whitebark pine on the Gallatin National Forest, Wyoming. Five years after planting, seedling survivorship dropped to 26%. Microsite conditions were critical in determining seedling establishment success in experiments in Wyoming. The best survivorship (45%) occurred on benches, and survivorship was poorest (2%) on swales (grassy depressions). McCaughey attributed poor survivorship on swales primarily to frost damage and pocket gopher (*Thomomys* spp.) herbivory, both of which were most common on swales. Seedling survival increased significantly when seedlings were protected from insolation by screens.

In my study, blister rust symptoms were not evident on transplanted seedlings at any of the sites, and blister rust was probably not a factor in seedling mortality. Blister rust does not usually infect whitebark and other five-needled pines until the sapling stage, when trees present a larger target for rust spores. Herbivory on seedlings was not evident at the northern Idaho and western Montana sites, but pocket gopher herbivory caused approximately 10% of total seedling mortality at the central Idaho site. Competition with grasses may have also lowered seedling survivorship there. Pinegrass and smooth brome (*Bromus inermis* Leyss.) were present at the study site, and by the second study year, smooth brome had expanded onto the study plots. Steele et al. (1981) noted that establishing conifer seedlings in clearings within subalpine fir/pinegrass habitat types in central Idaho can be difficult due to interference from rapidly growing grasses.

Western white pine is the closest relative of whitebark pine for which artificial regeneration data are available. Western white pine is classified in subsection *Strobi* of section *Strobus* (Critchfield & Little 1966). Like whitebark pine, western white pine populations have been greatly reduced by blister rust, and the primary goal of breeding programs for western white pine has been to produce plantation seedlings with genetic resistance to blister rust (Hoff et al. 1976, Hunt 1994, Mathiasen et al. 1993, Meagher & Hunt 1996). Breeding programs are proving successful for western white pine. On a northern Idaho plantation, 11-year-old saplings selected for blister rust resistance showed a 45% average blister rust infection rate 5 years after planting in areas of high rust infestation. Nonselected stock showed a 91% infection rate (Mathiasen et al. 1993). Estimates of family heritability of rust resistance traits range from 18 to 87% for western white pine (Meagher & Hunt 1996). Mechanisms for blister rust resistance are similar in western white and whitebark pines (Hoff & Hagle 1990, Hoff et al. 1994), and many aspects of breeding programs that have been developed for western white pine may be applicable to whitebark pine.

As I found for whitebark pine, western white pine populations appear to be broadly

adaptable to a variety of sites when transferred from their area of origin. Steinhoff (1981) compared survivorship, growth, and cold tolerance of coastal and inland populations of western white pine grown in northern Idaho. After 16 years, he found no significant differences between coastal and inland populations in any of the three variables even though seedlings experienced temperatures as low as -40°C . However, Meagher & Hunt (1999) suggested that important differences between western white pine populations might become apparent when they are planted near their northern geographic limit. In British Columbia, there were no significant differences in survivorship and height growth between coastal and inland western white pine planted on coastal sites, but survivorship and height of coastal populations was significantly reduced compared to inland populations when the populations were planted on inland sites.

My study suggests that there may be more among-population variation in growth characteristics for whitebark pine than for western white pine. Although the whitebark pine populations occurred within a single region, population effects for growth variables were strong. Whitebark pine populations appear to have distinct characteristics that may affect their adaptability when transplanted. Significant site \times population interaction effects for growth, aboveground mass, and biomass allocation variables indicate that mixing of genetically distinct populations may occur when blister rust resistant seed sources are transferred from area of origin and eventually interbreed with natural populations.

Between-population differences in growth are an important consideration when transplanting. For example, Rehfeldt (1983) predicted a 10% height loss when lodgepole pine seed is transferred 600 m above site of origin. Variation in cold hardiness in eastern white pine (*Pinus strobus* L.) is associated with latitude of provenance (Maronek & Flint 1974). In my study, height and stem diameter growth differed between whitebark pine populations ($P=0.0003$ and 0.0001 , respectively). Across sites, relative rankings of population means for height and stem diameter were more stable than rankings for other

variables (Figs. 2,3,4). However, there were no clear geographic or elevational patterns to population differences in growth. Seedlings planted near their origin did not necessarily outperform seedlings originating further north or south. On the central Idaho (wet) site, for example, the population from central Idaho (wet) showed superior height but poor stem diameter growth relative to the other three populations, whereas the northwestern Idaho (mesic) population showed moderate height and superior stem diameter growth on the central Idaho (wet) site. Steinhoff (1981) reported similar findings in his study of western white pine, in which there were interpopulation differences in sapling height but no clear geographic patterns to the differences.

For all populations, whitebark pine seedlings adapted phenotypically and reallocated biomass according to site. Growth rate is highly affected by biomass allocation of carbon to leaves vs. allocation to stems and roots. Even small increases in biomass allocation to stems or roots may alter growth rate greatly (Gower et al. 1995, Poorter et al. 1990). In my study, seedlings were taller, acquired more total aboveground biomass, and allocated relatively more biomass to leaves compared to stems on the wet site compared to the dry site.

The significant site \times population effect ($P=0.04$) for carbon isotope discrimination suggests that water-use efficiency in whitebark pine may have a genetic component, and that water-use efficiency can differ among whitebark pine populations planted in a common environment. High water-use efficiency typically confers drought tolerance (DeLucia and Heckathorn 1989, Ehleringer & Cooper 1988, Field et al. 1983, Sun et al. 1996). In my study, however, water-use efficiency of populations was not predictable based upon distance of planting from population origin, and did not match the climate from which the populations originated. For example, the northeastern Idaho (mesic) population showed greatest water-use efficiency on the western Montana (dry) site relative to other populations (Fig. 5). In contrast, the western Montana (dry) population had the least water-use efficiency relative to other populations on the dry site, despite

having originated in the area. Condon & Richards (1992) predicted that genotype \times environment effects for carbon isotope discrimination might increase when populations are moved to greatly contrasting environments. Differences in water-use efficiency between populations planted on the same site may become more important over time, or when populations are translocated to sites that are greatly different from that of their origin.

Studies of water-use efficiency for other conifers show that some species have significant among-population differences in water-use efficiency and drought tolerance. Genes that regulate either stomatal conductance or photosynthetic capacity should influence water-use efficiency by regulating c_a/c_i (Farquhar et al. 1989). For example, Zhang & Marshall (1995) found that when Douglas-fir (*Pseudotsuga mensiesii* (Mirb.) Franco) seedlings were grown in a common garden, coastal populations had significantly higher rates of net photosynthesis and stomatal conductance of water vapor, and lower rates of carbon isotope discrimination, than interior populations. Similarly, Monson & Grant (1989) reported higher rates of photosynthesis and stomatal conductance, and lower rates of water-use efficiency, in coastal ponderosa pine (*Pinus ponderosa* var. *ponderosa*) seedlings compared to interior ponderosa pine (*P. p.* var. *p. \times scopulorum* Engelm.) seedlings. Interior populations of ponderosa pine reduced water loss by reducing stomatal conductance, which increased c_a/c_i values and reduced net photosynthesis. Sun et al. (1996) reported significant differences in carbon isotope discrimination between family lines of white spruce (*Picea glauca* (Moench) Voss). They suggested that for white spruce, variation in water-use efficiency between families was due to inherent differences in photosynthetic capacity. Mechanisms that regulate water-use efficiency are unknown for whitebark pine.

Elevation has been shown to affect carbon isotope discrimination in some species, with carbon isotope discrimination decreasing with increasing elevation (Marshall & Zhang 1994). In my study, this relationship was not apparent for whitebark pine. Carbon

isotope discrimination decreased with decreasing elevation (Table 1, Fig. 5). While elevation cannot be discounted as a factor influencing carbon isotope discrimination in whitebark pine, site water availability appears to be more important.

Allozyme studies suggest that most genetic diversity of whitebark pine is among rather than within populations (Bruederle et al. 1998, Furnier et al. 1986). In my study, however, the significant site \times population interaction for a suite of adaptive traits suggests that there are important differences between whitebark pine populations. A clear geographic pattern to these differences was not apparent. Seedlings planted substantial distances from their area of origin showed good, and sometimes better, survivorship and growth rates relative to populations that originated near the planting site. Most importantly for restoration, seedlings expected to have greater than average resistance to blister rust were moved to climate regimes different from that of their origin without showing important differences in growth, biomass allocation, and water-use efficiency compared to native populations. This indicates that phenotypically rust resistant whitebark pine from areas with severe blister rust, such as northern Idaho, can be used as a source of rust resistant seed for plantings elsewhere in the northern Rocky Mountain region. The population from northwestern Idaho was particularly robust in terms of survivorship and growth, and would be a good candidate for artificial regeneration programs.

Translocation of populations should proceed with caution. This study followed seedling survivorship and development for only a short period. Between-population differences in development may become less important if the seedlings continue to adapt to their site as they mature, but if among-population differences become more pronounced, decreased vigor and survivorship may result. In areas where returning fire to the landscape is sufficient to restore whitebark pine, the potential impact of introducing other genotypes to naturally evolving populations is probably not warranted. In areas where decline of cone-bearing trees is so advanced that natural regeneration after fire is

sparse, planting blister rust resistant seedlings may help restore whitebark pine as a dominant member of the plant community.

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Table 1. Origin of the 4 study populations and location of the 3 study sites.

Location	Elevation (m)	Latitude (°N)	Longitude (°W)
Snowbank Mt. (central ID)	2380	44°29'	116°07'
Gisborne Peak (northwestern ID)	1690	48°21'	116°43'
Lunch Peak (northeastern ID)	1980	48°22'	116°22'
Saddle Mt. (western MT)	2380	45°42'	113°59'
Sheep Creek, ID (central ID)	2250	44°42'	115°34'
Sundance, ID (northern ID)	1400	48°37'	116°32'
Smith Creek, MT (western MT)	2286	46°30'	114°30'

Table 2. Long-term July climate means at population origins and study sites*.

Location	Daytime T (°C)	Ppt (mm)	VPD (Pa)
<u>Sites of population origin</u>			
Snowbank Mt. (wet)	16.4	1.4	1193.3
Gisborne Peak (mesic)	17.2	1.1	1029.4
Lunch Peak (mesic)	16.6	1.0	1019.5
Saddle Mt. (dry)	17.3	1.7	944.7
<u>Study sites</u>			
Sheep Cr. (wet)	16.7	1.2	1202.7
Sundance (mesic)	18.8	0.8	1127.5
Smith Cr. (dry)	16.9	1.7	983.4

*Based on MTCLIM (Hungerford et al. 1989) modelling of data from nearest weather stations. Weather stations nearest population origins are at Yellow Pine, ID, Priest River, ID, Cabinet Gorge, ID, and Hamilton, MT, respectively. Weather stations nearest the study sites are at Yellow Pine, ID, Bonner's Ferry, ID, and Stevensville, MT, respectively. T=temperature, Ppt=precipitation, VPD=Vapor pressure deficit

Table 3. Climate means for the 2 years of the experiment from weather stations nearest study sites (EarthInfo 1998, Western Regional Climate Center).

	Temperature				Precipitation				Snowpack		Relative	
	(°C)				(mm)				(cm)		humidity (%)	
	<u>1996</u>		<u>1997</u>		<u>1996</u>		<u>1997</u>		<u>1996</u>	<u>1997</u>	<u>1996</u>	<u>1997</u>
	<u>July</u>	<u>Ann.</u>	<u>July</u>	<u>Ann.</u>	<u>July</u>	<u>Ann.</u>	<u>July</u>	<u>Ann.</u>	<u>Ann.</u>	<u>Ann.</u>	<u>July</u>	<u>July</u>
Bonnars Ferry, ID	20.4	7.0	19.5	8.2	8.9	800.6	35.5	456.7	142.7	378.0	59.3	64.9
Stevensville, MT	19.5	6.4	18.1	7.3	10.9	467.9	33.0	367.3	233.9	60.4	62.1	62.1
Yellow Pine, ID	16.4	4.5	14.5	5.3	11.4	1007.6	47.2	628.9	214.1	470.2	62.1	69.4*

*Relative humidity data were not available from Yellow Pine and are given from nearby McCall, ID.

Table 4. ANOVA table for growth rate variables (n=663).

Source	df	<u>Height</u>			<u>Stem diameter</u>		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Site	2	72.50	11.07	<0.0001	17.07	20.27	<0.0001
Population	3	41.79	6.34	0.0003	9.04	10.53	<0.0001
Site×Population	11	32.70	5.1	<0.0001	6.06	7.50	<0.0001
Error	1384	19.45			2.52		

Table 5. ANOVA table for biomass allocation and carbon isotope discrimination variables (n=144).

Source	df	<u>Total mass</u>			<u>Stem allocation</u>		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Site	2	7.23	13.56	<0.0001	0.03	5.98	0.003
Population	3	1.52	2.50	0.062	0.008	1.38	0.20
Site×Population	11	2.05	4.03	<0.001	0.01	1.85	0.05
Error	413	1.65			0.018		

Source	df	<u>Leaf mass ratio</u>			<u>Leaf area ratio</u>			<u>¹³C: ¹²C ratio</u>		
		MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Site	2	0.35	6.02	0.003	0.82	3.10	0.05	23.29	7.45	0.0008
Population	3	0.009	1.40	0.25	0.97	3.76	0.01	1.59	0.46	0.71
Site×Population	11	0.01	1.86	0.05	0.62	2.52	0.006	6.09	1.91	0.04
Error	413	0.018			0.77			9.66		

Figure legends

Figure 1. Percent survivorship of four populations of whitebark pine on three study sites 1 and 2 years after planting. N=90 seedlings/population/site.

Figure 2. Height and stem diameter of four populations of whitebark pine at three study sites. Data are means and one standard error.

Figure 3. Aboveground biomass of four populations of whitebark pine on three study sites. Data are means and one standard error. N=12 seedlings/population/site.

Figure 4. Leaf mass ratio and leaf area ratio of four populations of whitebark pine at three study sites. Data are means and one standard error. N=12 seedlings/population/site.

Figure 5. Carbon isotope discrimination for four populations of whitebark pine at three study sites. Data are means and one standard error. N=12 seedlings/population/site

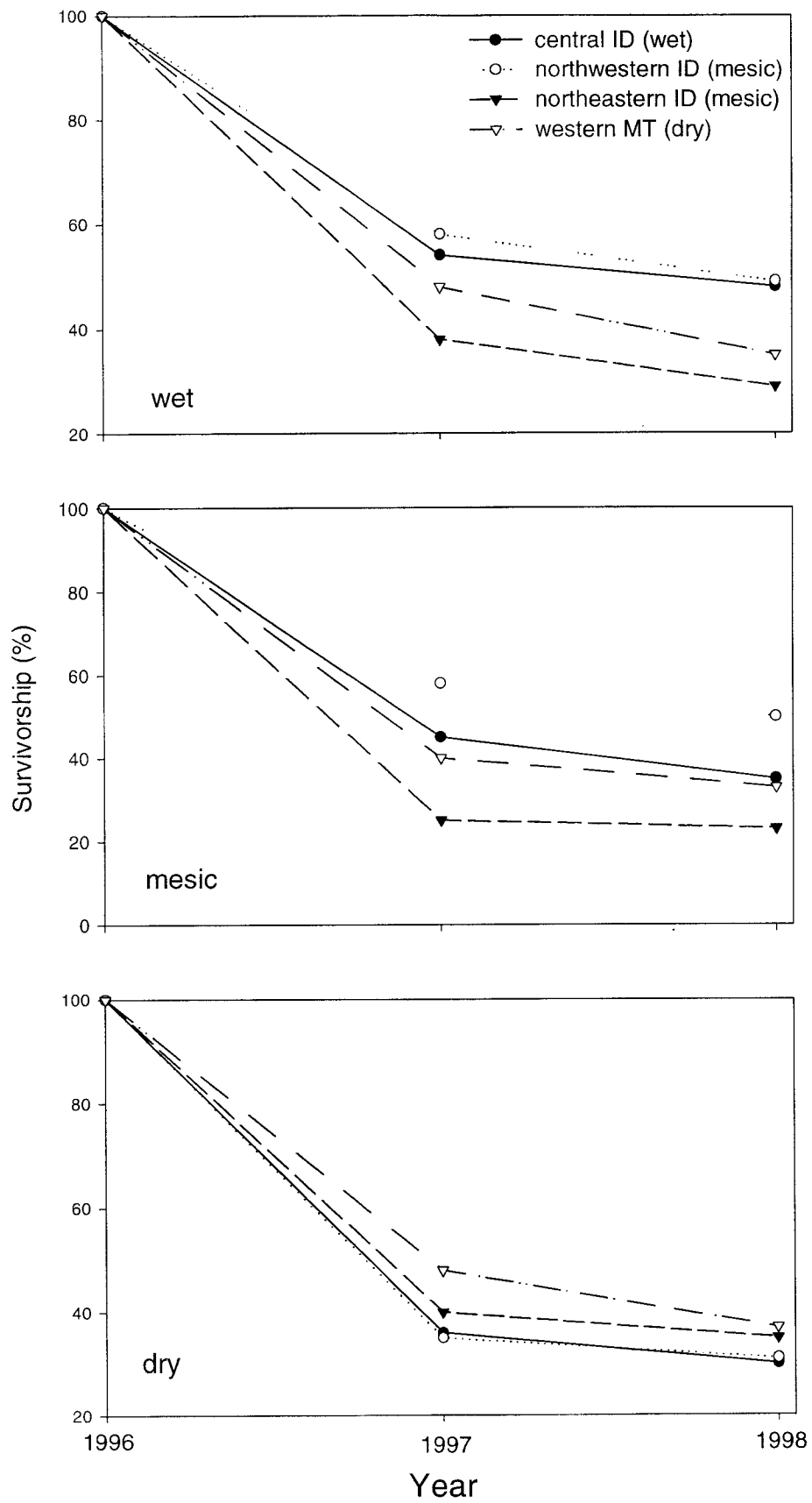


Figure 1

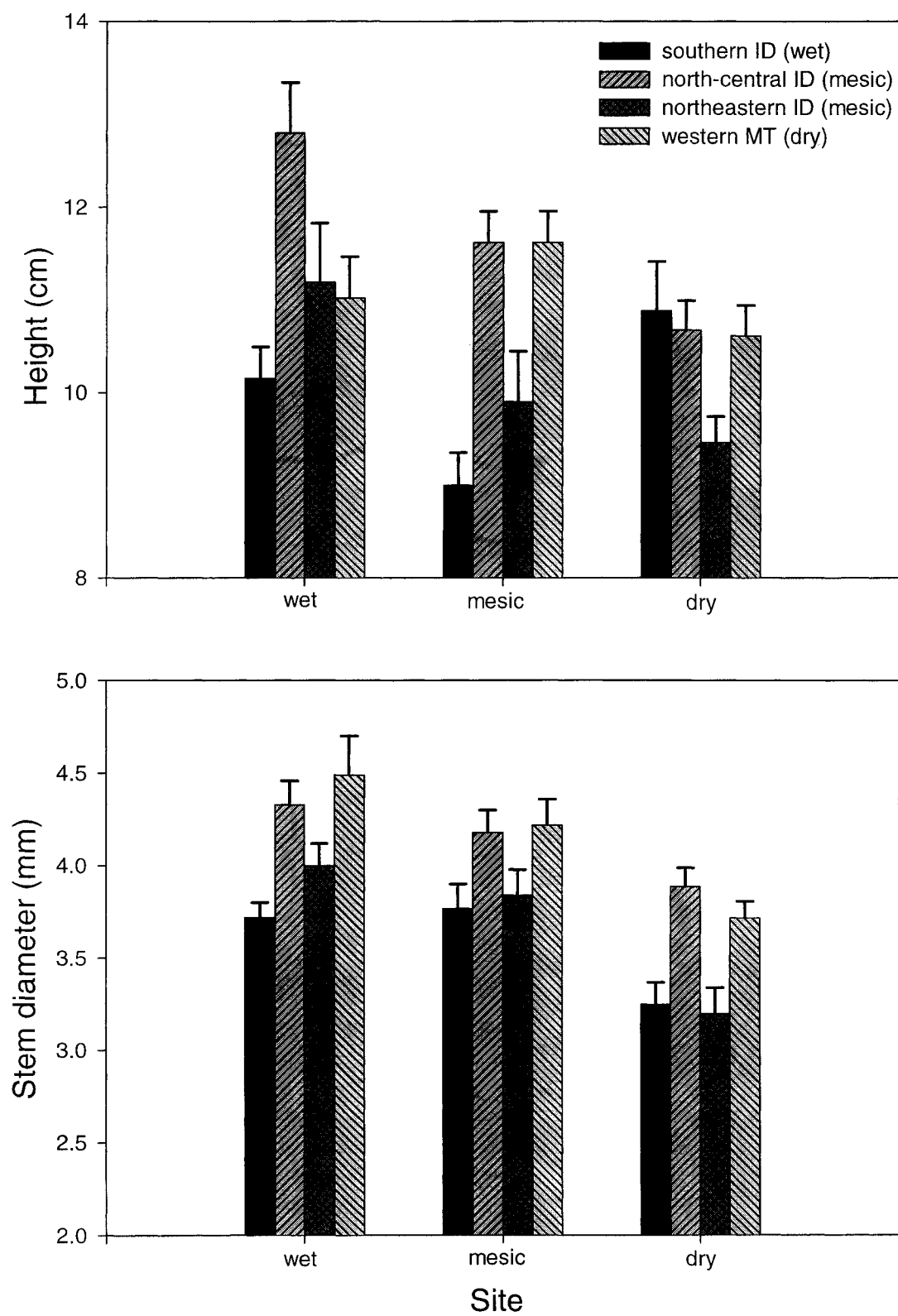


Figure 2

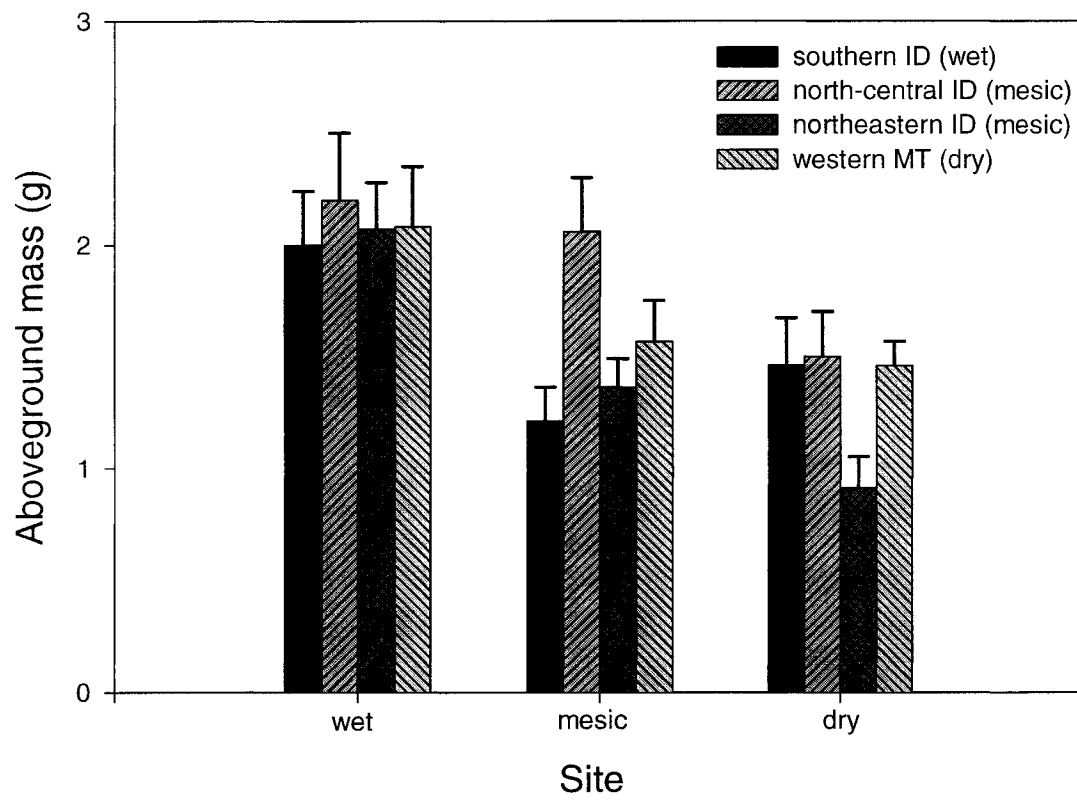


Figure 3

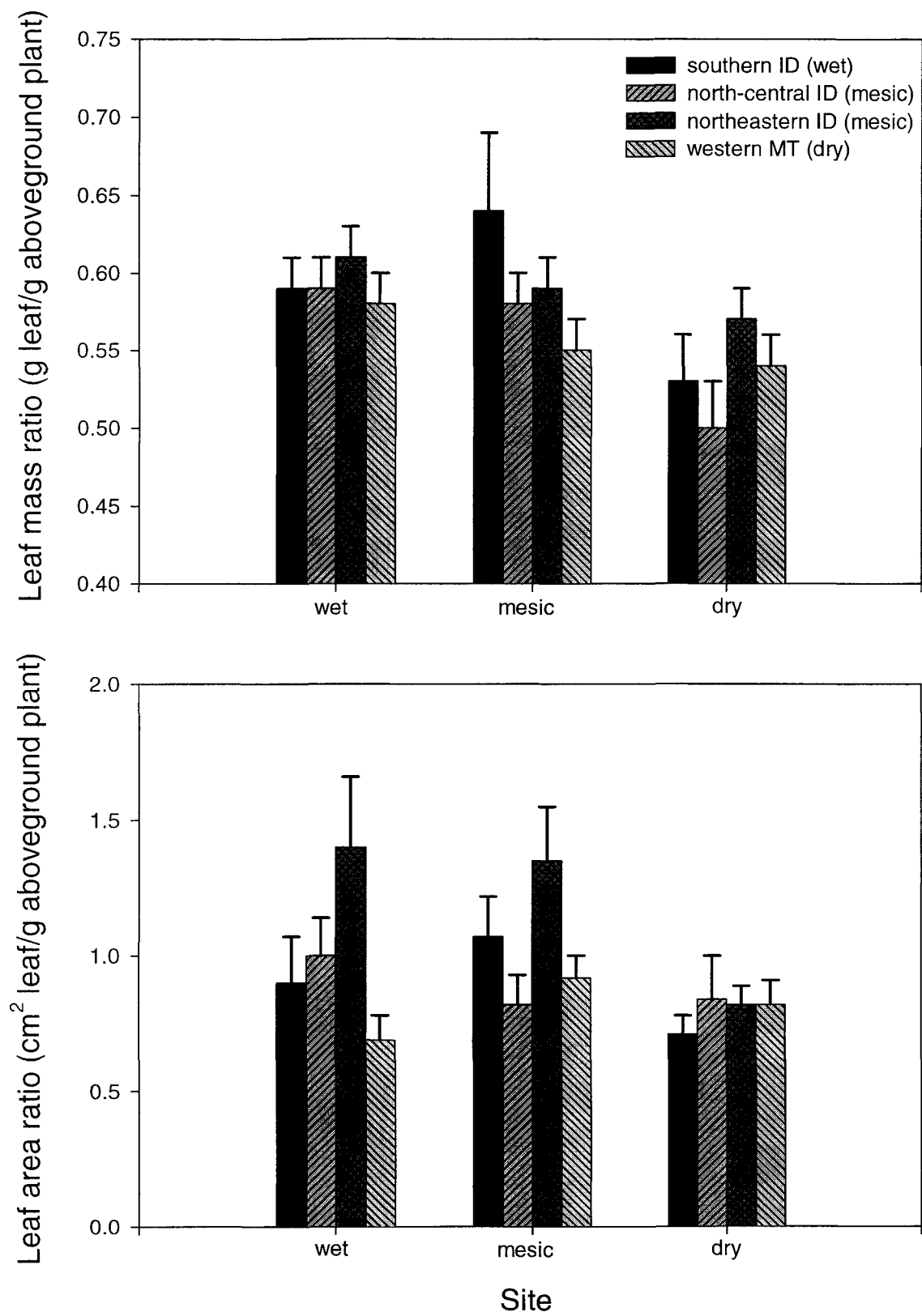


Figure 4

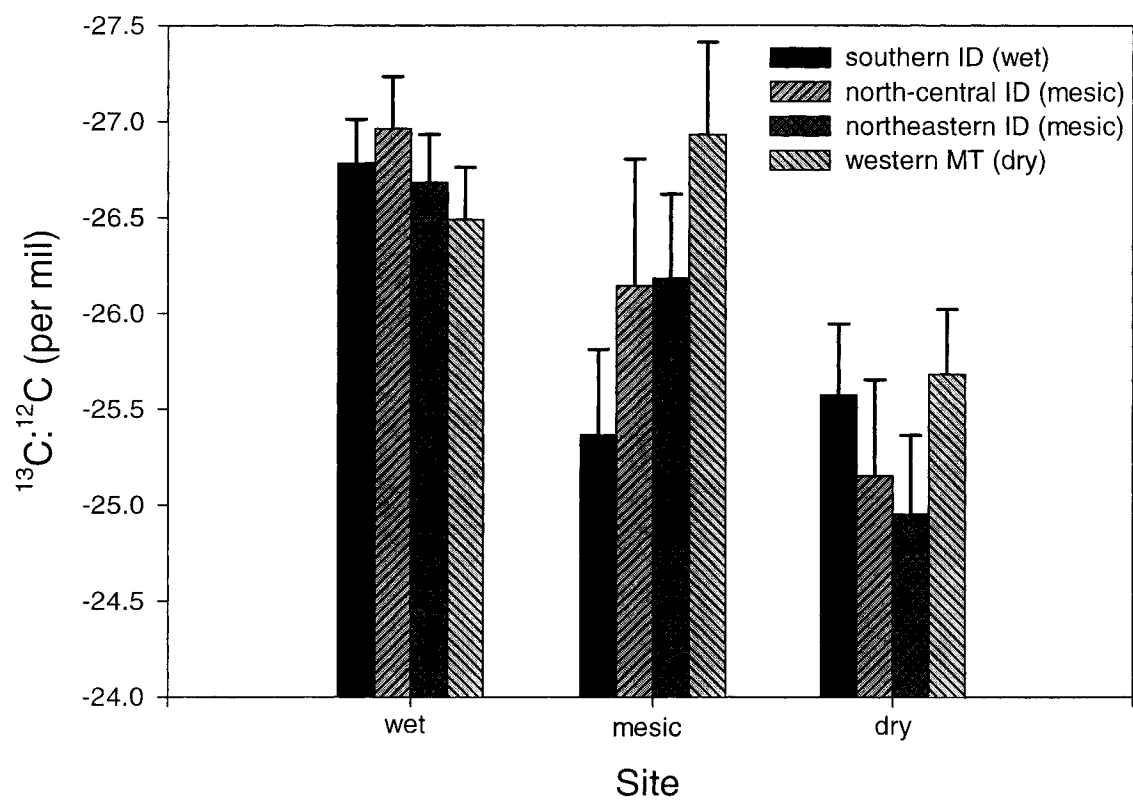


Figure 5